Basic Course in Ornithology
Dr. Manjari Jain
Indian Institute of Science Education and Research, Mohali

Lecture -15
Vocal Behaviour: Mechanisms (Part 2)

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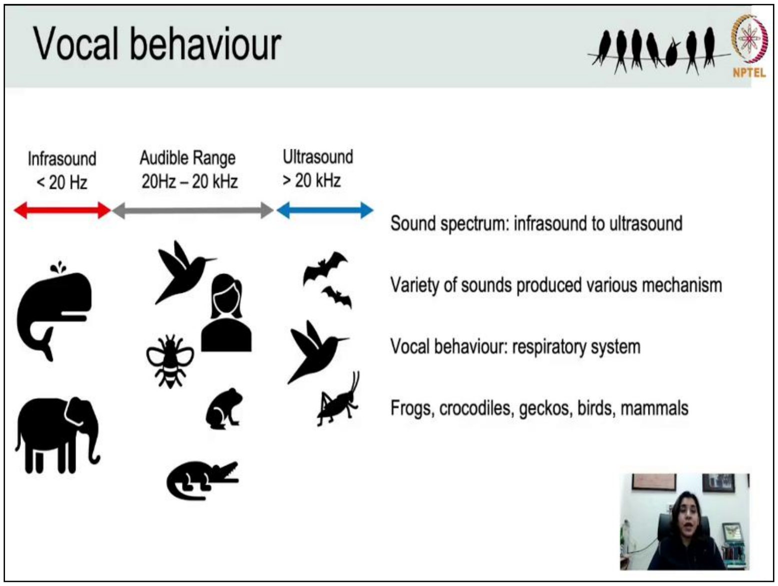

Welcome viewers to the basic course in ornithology. Today's lecture is about vocal behaviour in birds; the mechanisms involved. I am Dr Manjari Jain from IISER, Mohali. Animals across various taxa use sound to communicate but when we say sound, it could be sounds that we can hear or we can't. The sound spectrum is divided into three parts infrasound, the audible range and ultrasound. Infrasound includes all sounds that are produced that have frequency below 20 hertz.

The audible range includes sounds within 20 hertz to 20 kilohertz frequency whereas ultrasound is sounds with frequency which is higher than 20 kilohertz which we can't hear. As you can see in this schematic, various different groups of animals occupy different parts of the auditory system spectrum and larger bodied animals such as whales and elephants can produce infrasonic signals whereas other animals such as other well other mammals, various species of birds, many insects, frogs, some reptiles, they all utilize the audible range of the auditory spectrum.

So, this part of the auditory spectrum is rather crowded. Ultrasound of course is produced mainly by bats, several insect species - Katydids and some birds like Oilbirds and Cave Swiftlets. Now, birds are incapable of producing infrasound but recent evidence shows that they may be capable of hearing some infrasonic frequencies. At least some birds may be able to hear infrasonic frequencies. Surely, some of you have heard birds in your neighbourhood and after this lecture I would urge you to go out and listen to birds in your neighbourhood and try to decipher how many different kinds of birds can you recognize just by their sound. But you must have definitely heard Pigeons fly, the fluttering of pigeons or some other birds when you just run and approach them they suddenly fly. So, that flapping of the wings produces a particular sound, the tapping of their feet on a substrate or snapping of the bill all of this produce sound but none of these can be termed as vocalization.

And the term vocalization has a specific meaning. It specifically refers to sounds produced by expelling air from the respiratory system. In fact, only vertebrates are capable of vocalizations although a much larger variety of species are acoustically active. So, when I say the insects can produce sound in the ultrasound range or insects are producing sound in the audible range, they are not producing vocalizations. These cannot be termed as vocalization, because insects produce sound by a very different mechanism which is called stridulation. The mechanism by which birds like many other vertebrates produce sound, the central point being that air has to be expelled from the respiratory system. So, that is required and as I said many species of vertebrates can vocalize and these include frogs, crocodiles, geckos, birds and of course many different kinds of mammals.

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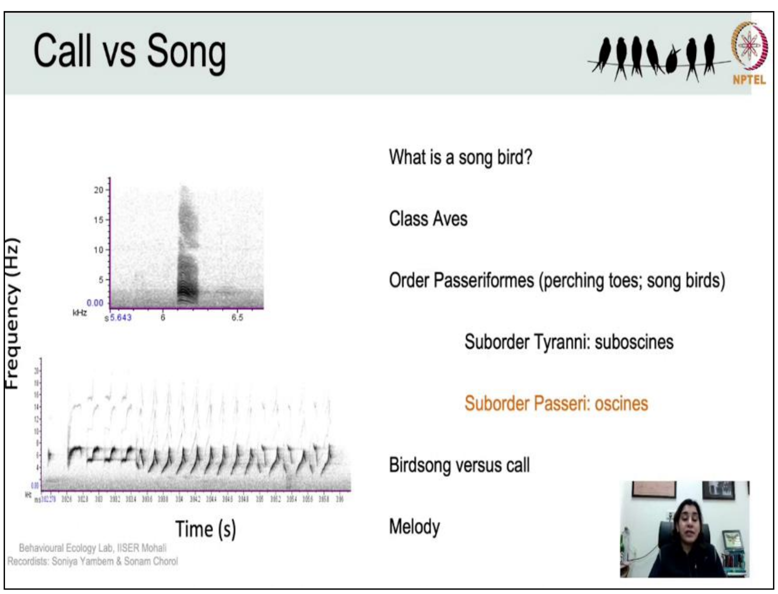

So, now let us try to understand when we refer to bird song, let us first ask the question what is a song bird? Many species of birds are capable of producing various kinds of vocalizations but only a small set of these group of birds about 10,000 species of birds found in the world. A very smaller subset of this can actually produce elaborate sound what we call as songs which have complex acoustic structure and are produced mainly during the breeding season. These group of birds are called songbirds.

Songbirds are very diverse and they are they comprised of about 45% of this 10,000 species of birds that are found in the world. So, now 45% is a very large fraction but remember only 45% of these 10000 species of birds are actually song birds, not all birds are songbirds. Now all songbirds belong to the order Passeriformes. So, do all birds that belong to the order Passeriformes which are basically birds that have this perching toes can we call all of them as songbirds? No.

Not all birds that have perching toes can be considered as songbirds. Under the order Passeriformes we have two sub-orders one belong to suboscines which also produce vocalizations but they are not song birds. Only birds that fall under the sub-order passeri are called songbirds or oscines. Now the reason why bird songs are special is because they have better control over the way they produce sounds - a better syringeal control.

Now, let us think of the larger body of birds in general. Many birds vocalize, not all produce complex sounds but they are vocalized or rather many birds vocalize. And bird vocalizations can be of two kinds - calls and songs and how to distinguish between them? An easy way to distinguish is that songs are typically longer bouts of vocalizations but produced in a limited context.

Think about the territorial display, the sound that birds produce when they are defending a territory. It is a display sound or birds that produce courtship songs to attract mates. These are two major contexts in which songs are produced. These would be the limited context in which song is produced by birds. Calls on the other hand, last for a very short duration. So, they are shorter vocalizations but they are produced or can be produced in a variety of contexts.

The other important thing to note is that songs are typically melodious with a complex acoustic structure. Calls on the other hand are not melodious, they lack the complex acoustic structure.

Songbirds can produce both songs and calls and birds in general outside of songbirds they all produce various kinds of vocalization which may sound melodious to you but that does not make them a songbird. Now to make my point more clearly let me ask you to think of the vocalizations of a Robin versus that of a Crow.

The melody in a sound arises from specific acoustic features such as the change in frequency, the presence of harmonics which is basically how frequencies are combined (the way in which they are combined), presence of a rhythm which is which refers to the temporal structuring of elements and the performance technique as well as the sequence in which the elements are produced and they are repeated all of these contributes to the presence of melody.

Now that does not mean that vocalization have to be melodious for us humans for the bird to be a songbird. Both the Robin and the Crow are songbirds even though one might argue that the Crow does not really produce songs. So, why are we calling it a songbird? Well, song birds are a taxonomic group which is not a melody based classification but more of how they have vocal control. So, that is one thing I would like all of you to keep in mind and the all song birds are oscines.

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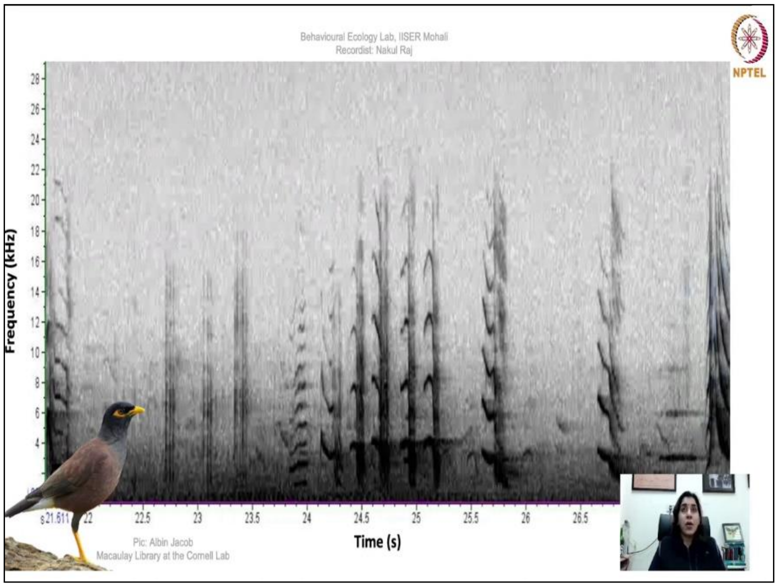

So, now let us listen to the song of a bird. What you are hearing is the vocalizations of a very common bird - the Common Myna. You all must have heard the Myna in your neighbourhood, in your balconies, near the windowsill, in the garden around you basically, bus stops wherever they are found very they are basically found everywhere and they have a close association with humans. So, if you notice this plot that I am showing here is a spectrogram which tells us how sound is distributed over various different frequencies and across time.

And it tells us how the sound of the bird looks like. So, if you want to visualize sound this is the way to do it. A spectrogram (plot shown in the slide) also allows us to see the variation in the elements that make up the song or the vocalizations of birds. So, it is a very powerful and very useful way to look at sound and to analyze it. And those of you who are interested in bioacoustics and bird sound would I would really recommend that you record some bird calls with your mobile phone maybe of the Common Myna and download Raven (sound analysis software) maybe from the website (a trial version is free) and you can visualize these sounds using a spectrogram.

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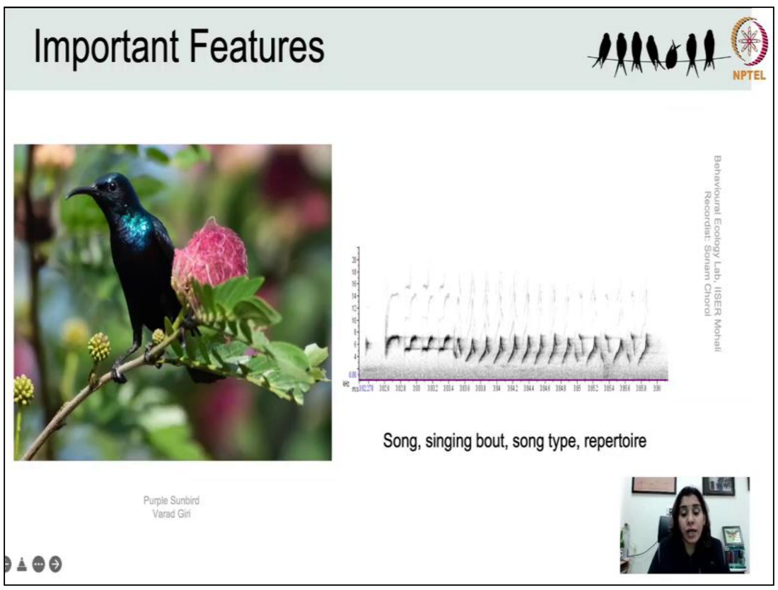

Now here what I am showing you is also a spectrogram only, I have taken a small section of the vocalization of another very common bird which is the Purple Sunbird. Now, the recording that I am showing you these were recorded on IISER, Mohali campus. And what I am trying to show you here is what the song of the bird actually comprises of and how can we study these songs. So, the smallest or the shortest or the simplest acoustic element in the song is called a note.

Notes when uttered rapidly and when they have very different frequencies of vocalization and if they are produced at almost the same instant are known as syllables. So, here you can see a syllable, here you can see that two notes towards the end which I have marked of the box that I have marked you will see those two notes have very different frequencies yet they are almost at the same instant they have been produced.

This is possible in birds because of the dual syrinx mechanism that you already have learnt about and the tiny silent interval between the two notes of the syllable is the mini-breath. Many notes and syllables combine to form what we call as a phrase. Now, both calls and songs have notes and phrases. It is not that only songs have phrases and calls do not have phrases. Calls can be of a single note but they can also be of multiple notes combined together to form a phrase structure.

But only songs have complex features like the syllables and the mini-breath. Further, a song is comprised of multiple phrases - a repetition of the same phrase. So, you can have many different kinds of phrases which are sort of combined together to form what we call as a song and many different phrases are delivered over a longer period of vocalization and which is known as a song bout.

So, one time period over which these various phrases are being produced is known as a singing bout or a song bout. A single individual of a bird species can have different song types which basically mean that they are composed of different kinds of phrases. So, the same individual can have multiple song types. And the collection of all song types for an individual bird is known as its repertoire.

You can also look at the repertoire of the species which would be all the song types produced by individuals of these species. So, there will be multiple individuals you need to account for all of those songs that would be the repertoire of a species. Now, about 30% of all songbirds have only a single song type whereas another 20% of the songbird species have repertoires which include more than five song types.

So, having multiple song types is not that common and then of course there are some extremes such as the Brown thrasher who have more than two thousand song types in its repertoire. Now, let us listen to some calls and songs of birds and I have chosen some really common birds -common Indian birds so that you can relate to these vocalizations.

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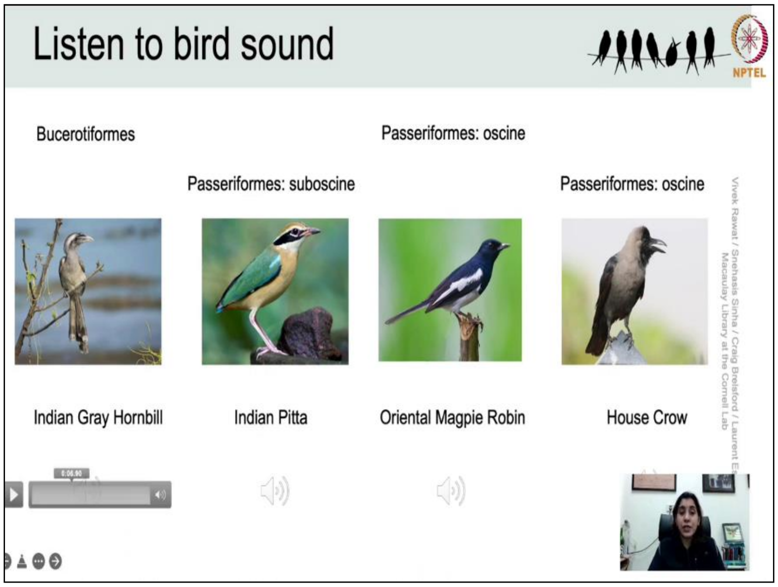

The first one is that of an Indian gray hornbill, this is not a song bird in fact it is not even under the order Passeriformes but it does vocalize. Now, we will listen to a bird that falls under the order Passeriformes but is not a songbird is a suboscine say Indian Pitta. So, that is the Indian Pitta, not a songbird. Now, let us listen to a songbird the Oriental Magpie Robin. I hope you could hear the many different kinds of notes it is producing the complexity of the acoustic structure or the vocalization in this bird.

On the other hand, the melody of course, let’s listens to the House Crow. Now this is hardly melodious but remembers melody cannot be the criteria for defining a bird as a songbird or not.

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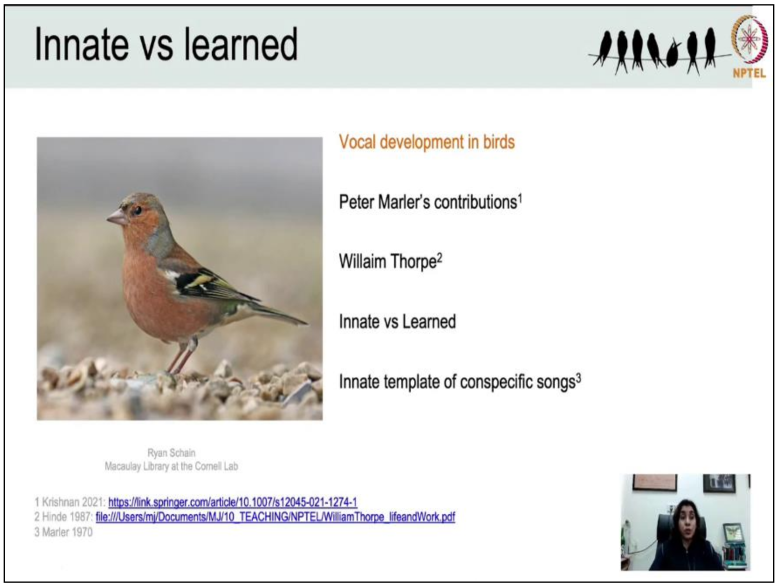

Now, let us talk about how do the birds know what to sing? Like many other behaviours, vocalization or singing can also be innate or instinctive or learned. Peter Marler was one of the most famous ornithologists who contributed significantly to the advancement of the field of birdsong research and you can read about Marler's contributions to this field in a very nice article written by my colleague Dr Anand Krishnan.

The article is freely available published in Resonance of Indian academy of science and the link to the article I have put in this slide (https://link.springer.com/article/10.1007/s12045-021-1274). Now while Marler's contributions were significant enormous in fact in this field, the field of birdsong research was pioneered by William Thorpe in 1950s. Thorpe was an entomologist to begin with (well entomologists are scientists who work on insects) but was also very interested in instinctive behaviour versus learned behaviour and was strongly influenced by the nobel laureate Konrad Lorenz.

In the 1950s, he made seminal contributions to the field of vocal development in birds asking the questions whether bird vocalizations are innate or learned? And the answer to that question is that vocalizations in birds can be either innate or learned. And these vocalizations may be evoked by sexual cues, for instance, the presence of a rival male in the vicinity or presence of a potential mate in the vicinity or by emotional states such as fear due to the presence of danger.

Now, the majority of avian species produce only innate vocalizations that are hardwired meaning that they occur spontaneously in response to certain relevant stimulus. Specific brain structures regions in the brain and underlying genetic programs control production of vocalizations and the innate vocalizations are produced with little or no environmental influence. This basically means that they cannot be learned through social interactions or by practice.

This is largely true for all suboscines and there are a few exceptions like parrots and hummingbirds but apart from these exceptions suboscines do not go through the process of song learning. In contrast, oscines or songbirds learn bird songs through vocal development and this involves young birds listening to a model sound from their tutor and this tutor could be a male bird in their vicinity or their own father.

And then memorizing the model song and practicing to produce similar sounds which match this match with the model sound. Until they produce sound which basically the template matches completely or more or less. Thorpe showed using a host of laboratory experiments using Chaffinches who were isolated early on from their conspecific adult males who could be their potential tutors during development of song will not develop a normal song they will develop an abnormal song.

But if these isolated Chaffinches are exposed to tape recordings of wild Chaffinch song then they will developed male song which basically demonstrate the demonstrated the fact or prove the fact that birds such as the Chaffinches must learn the birdsong early on in their life. So, there is a critical period when which they should learn the bird song. Although, they learn songs from their tutors, birds already have an innate template of what the song of their own species is so.

Even birds the oscines who go through song learning it is not they learn from scratch, there is a pre-existing template of what their own species call is like. And Marler showed using White crowned sparrows that when presented with tutors who are both conspecific and heterospecific. The young ones the young White crowned sparrows will only learn the calls of their own species or they will use the tutor of their own species.

Now this mechanism of picking up having an innate template of what your own call must be like. So, the species-specific song this must have evolved to avoid errors and mixing identification of conspecifics from heterospecifics. Of course, this is not foolproof, but by and large it is there, which basically means that there is an innate template two conspecific songs even in birds that learn the songs and they do not have an innate song per se.

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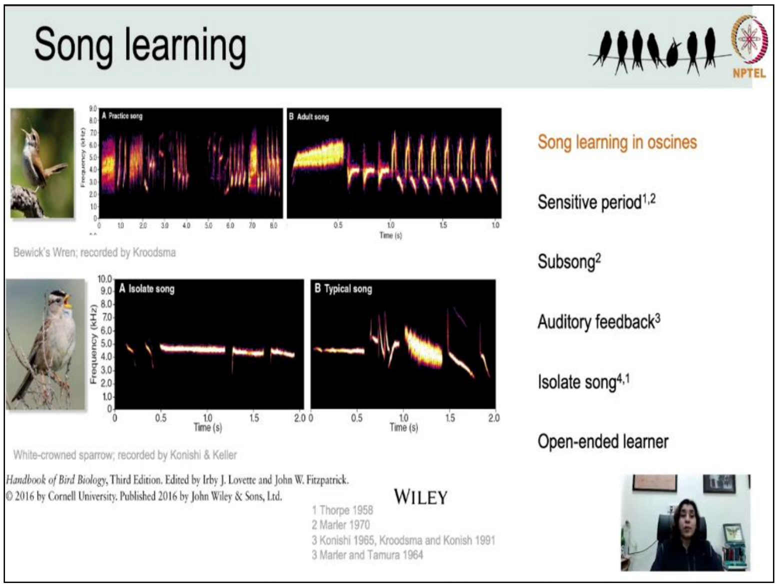

Now let us talk about song learning and the process that underlies song learning in and of course by that I mean specifically for oscine. So, the period of time during a songbird's neural development when it is able to learn the song from a tutor is known as the sensitive period. During this time young birds may produce what we call as practice songs which are referred to as sub songs.

And the practice may begin at the nest but most often than not it is completed much after they leave the nest. They practice the song till the sub songs match the actual song. So, the model is there first there is an innate template of what conspecific song is like, they hear the model songs from the tutor during the sensitive period and then they practice. While they are practicing, they produce what we call as sub songs and eventually the songs that they deliver would match the actual model.

So, the presence of a tutor is very important and it is equally important for the birds to be able to hear itself while it is practicing to sing a proper song. Now, this has been demonstrated by experiments using young White crowned sparrows. What they did was basically took young White crowned sparrows and they were deafened/surgically deafened. So, that they do not have an auditory feedback. So, they cannot hear themselves sing and such birds (the White crowned sparrow in this case) developed abnormal or aberrant songs.

So, basically it goes on to show that auditory feedback is essential for songbirds to develop normal song. On the other hand, when they did separate similar experiments (by a different group of people of course) on Eastern Phoebe which is a suboscines species that lacks vocal learning, when they deafened the eastern phoebe and therefore it did not have auditory feedback, it still went on to develop the normal song despite not having the auditory feedback which basically goes on to show that their songs are innate and they are not learned.

Now, generally birds that possess a sensitive period of song learning acquire the song repertoire in within the first year of their life itself and rarely go on to modify it. And White crowned sparrow are one such species and there are some other species which include Common chaffinches, Marsh wren so on and so forth. For a White crowned sparrow this starts this learning process starts approximately on the 15th day post hatching and lasts from up from the 15th day to up to 50th day.

And if the tutor is absent or is removed from the young bird then what the young one developed is what we call as an isolate song. So, when the young bird is isolated from the tutor during this period when it is learning it develops a song. It is not that it will not develop a song and that song is known as an isolated song. And this song, of course is abnormal and like we said if it is deafened and it cannot produce a normal song.

The same was also demonstrated in Chaffinches by William Thorpes. So, the presence the or the importance of the presence of a tutor and the importance of auditory feedback both were demonstrated using classical experiments in this field by Peter Marlar on White crowned sparrows and on chaffinches by William Thorpe. One last thing that I want to talk about is about open-ended learners.

So, I talked about the songs which are then developed and it matches the template and that most often than not these songs are not updated but there are songbirds that are capable of learning new songs throughout their lives and these are called open-ended learners and an example would be the Northern mockingbird and the Common nightingale. So, this is just to keep in mind that while song development happens in this way and that most often they develop and get their final song by the end of this period. There are species of songbird that can continue to learn new songs through their life.

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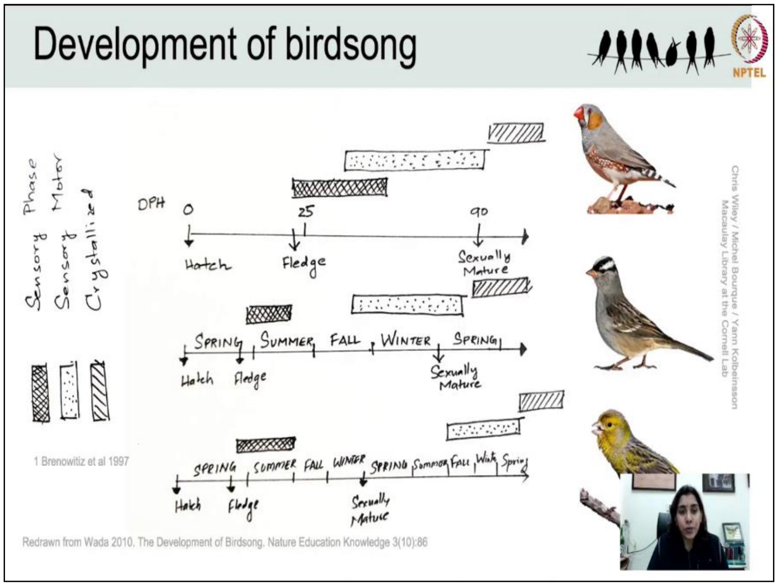

Now let us get into the details of development of bird song. This schematic what I have drawn is to show the timeline of bird song development in three different species I have used Zebra finches then I have the second one is the White crowned sparrow and I have used the Canary to give the example. There are three different phases that I have highlighted with three different kinds of marking the first is the sensory phase / the sensory motor phase and finally what I call is crystallize is when the song is crystallized. So, let us talk about this a little bit.

So, bird song learning occurs in two distinct stages - the sensory and the sensory motor phase. During the sensory phase young birds memorize their tutor's song and form an auditory memory or a template. Remember there is a pre-existing innate template of what its own species call is like.

And on top of that during the sensory phase by listening to their tutor they form an auditory memory of the tutors song or the model song template.

Later during the sensory motor phase, young birds start producing generic variable and soft vocalizations which are called as sub songs. The sub songs are the songs that they produce in the sensory motor phase and these are not structured and these are not the final song these are more very variable and are more soft vocalization and similar to babbling in humans if you like. Then they produce louder and more structured song that are still different from the final song that they will go on to produce.

And these louder a little more structured songs are called plastic songs. They then translate the inner template that they have of this auditory memory of the tutors song into motor activity by practicing and comparing their vocalizations to the template. So, this is where the auditory feedback is important. And refining that the sound refining the sound that they produce with practice eventually to produce what we know what we call as the crystallized sound which basically a stable song similar to the model songs of course these finals crystallized song that the bird produces will not be the exact copy of that of the tutor. They will have their own variations in the individual variations in it but the point being that the crystallized sound is more or less similar to the model sound that they learned during this during this song learning phase.
So, now during the sensory motor phase it is therefore it is very important for the birds to be able to not just hear the tutor but to remember to make an auditory memory of that and also to get the auditory feedback by hearing themselves like we just discussed that it is important for the birds to be able to hear themselves so that they can crystallize, they can leave out some kinds of sub songs that they have produced and use a smaller subset of the plastic song that they are they produce to form the final crystallized song. Last but not the least, the hormone testosterone of course, there is the entire matter about the endocrine you know control of birdsong learning and the hormone testosterone has been found to be important for song crystallization in order to reduce song plasticity.

So, the many variable kinds of songs that they were producing during the learning phase finally of that very large set of songs that they produce, they select a smaller set of the songs that they produce during their practice phase to make the final crystallized sound. How exactly do they select and what determines which the plastics of which kinds of the plastic songs that they produce they will use? That is not very clearly understood.

So, here as you can see the Zebrafinch, what I have shown in the timeline is days post hatching so DPH's days post hatching from the time. It hatches to about 25th day that is when the sensory phase of the Zebrafinch starts by now it has already fledged. Same thing for the White crowned sparrow, it is fledged when the sensory phase starts this is when it is listening to the tutor's song. Same for the Canary after fledging the sensory phase starts.

The sensory motor phase as you can see for the Zebrafinch kind of overlaps with the sensory phase. It does not overlap for the White crowned sparrow nor does it overlap for the Canaries. And you can see that once this actually mature that is when the song crystallization happens. So, sexual maturity happens in case of the Zebrafinch and that is when the sound crystallization happened. For the White crowned sparrow the sensory motor phase goes on till the beyond the sexual maturity.

So, this keep on learning and crystallization happen much later and similarly for the for the Canaries of course the sensory motor phase itself sort of starts after sexual maturity and crystallization much later. So, what I am trying to depict here is that while the three stages or rather the two major stages of sensory and the sensory motor stage and final we can call it a stage the crystallization part of the song it is common across all of these songbirds. But the way and the timeline that each bird will follow is varies from species to species.

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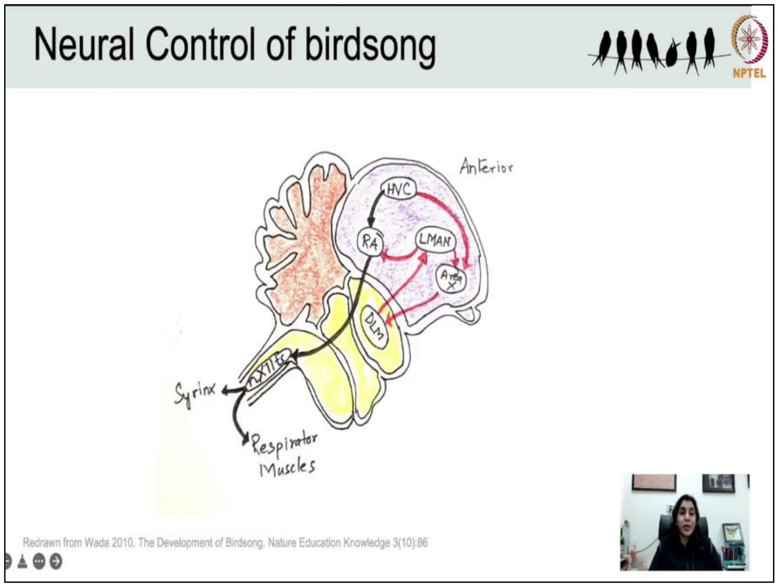

Now, let us look at the neural control of birdsong and for the purpose of this lecture, we will not go to the great details but very peripherally. We will try to understand what parts of the brains are important for bird sound production and what pathways may be important just to get you a flavour of this area. So, bird song is controlled by specific regions of the brain which are interconnected as you can see in the schematic that I have provided here.

Now there are two neural pathways that are needed for song production and learning. The first is called as the motor pathway and the second is the anterior forebrain pathway or the AFP. The motor pathway is responsible for song production as it influences the motor control over song production and the AFP is crucial for song learning and plasticity. In this schematic of the brain presented here, the black lines depict the motor pathway and the red lines depict the anterior forebrain pathway.

The region of the brain called HVC or the higher vocal complex projects to another region of the brain called array which sends neurons to the vocal organ of the bird the syrinx and the respiratory muscles thus allowing the bird to be able to sing while also breathing. So, it really controls the motor or the mechanism by which these muscles will act thereby allowing the bird to continue to breathe while they are singing which also allows them to sing for a long period of time.

Neural anatomical studies where surgically parts of the brain were lesioned in birds to deactivate certain specific regions have helped us to understand the function of the anterior forebrain pathway. What was found was that if the songs have already been learned and if the lesions or the surgery is done after songs have been done then reactivating parts of the brain will not affect already learned songs. However, any lesions to these regions which are involved in song learning and plasticity before song crystallization.

So, if lesions happen before song crystallization this would result in abnormal songs. So, this should give you a flavour of how bird songs are produced and what are the neural mechanism underlying it all right.

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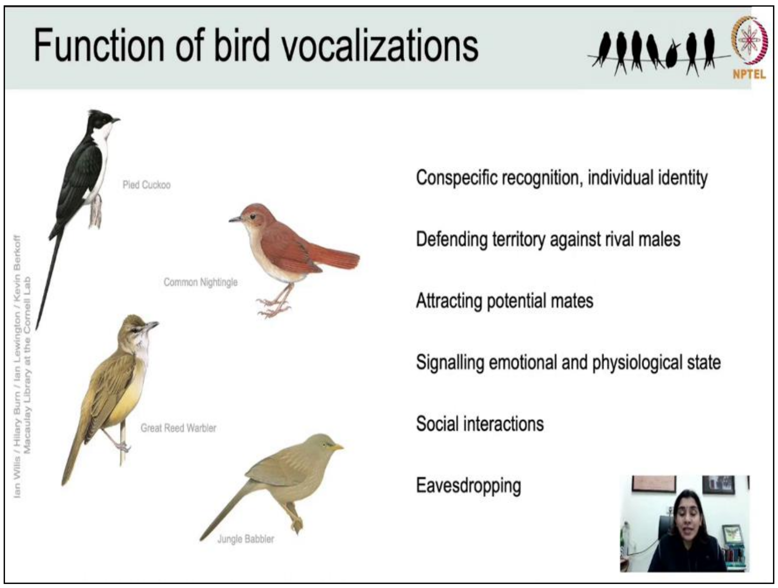

So, last but not the least, let us talk about the function of bird vocalization. Bird vocalizations both calls and songs serve many functions. First and foremost, they allow conspecific recognition and may even code for individual identity in some cases. Bird song is specifically as we discussed earlier used as a display for defending territories against rival males and hence mediates male-male competition but it is also used as a display in intersexual communication serving as a courtship display or courtship signal to attract potential mates.

In fact, it is well known that bird song is strongly driven by sexual selection both via male-male competition and female choice. Bird calls serve many functions as we discuss songs have limited context and function whereas bird calls can be used in many different contexts. And they serve many functions such as signaling emotional states such as distress or alarm. Signaling physiological states such as hunger, mediating social interactions within group members and providing basically providing a rich source of informations to specific or intended receivers.

Now here I have put the images of four different bird species - the Pied cuckoo, the Common nightingale, the Great reed warbler, and the Jungle Babbler. The Pied cuckoo is not a songbird, the others are. While Jungle Babbler is a songbird it produces calls and not songs The nightingale produced song in the context of mate attraction whereas the Great read warbler produces song in the context of territory display.

The Pied Cuckoo as you know is a brood parasite and it lays its egg in the nest of some species of Babblers including the Jungle Babbler and therefore, I want you to think would its vocalization be innate or learned. I think you know the answer by now. So, now last but not the least what I want to talk about is eavesdropping in birds. So, bird vocalization can be eavesdropped by other unintended receivers who may extract information from the signals to their benefit and occasionally to the disadvantage of the senders.

For instance, if a bird is producing an alarm call, other birds may use that information to also understand eavesdrop on that information on the signal to extract the same information or they may use the sound of the bird predatory birds may extract information of the presence or the location of an individual based on its vocalization. So, a Jungle Babbler may be vocalizing for a completely different context intended towards its own group members but there might be a Kite hovering above who may use the sound of the Jungle Babbler to localize its position. So, that would be eavesdropping.

So, the studies of bird vocalization is a fascinating subject and in India it is still a very nascent field but faculty from three different IISER including myself are working extensively on the bioacoustics of birdsong to address questions in ecology, in behaviour and evolutionary biology. I hope you will be interested in bird song and the research as well and do feel free to write to me if you have any further questions. I am Dr Manjari Jain from the Behavioural Ecology Lab from the department of biological sciences at IISER, Mohali. Thank you.